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Phylogeny and Checklist of the Nocturnal Tiphiids of the Western Hemisphere (Hymenoptera: Tiphiidae: Brachycistidinae)

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Abstract.—Phylogenetic relationships among eleven genera of Brachycistidinae (Tiphiidae) are discussed, based on male characteristics, and a key to the genera is provided. The genus *Stilbopogon* is found to be the sister group of the rest of the brachycistidine genera. There are two well supported clades: *Brachymaya* + (*Hadrocistis* + *Brachycistina*) and (*Paraquemaya* + (*Brachycistellus* + (*Dolichetropis* + (*Sedomaya* + (*Brachycistis* + (*Acanthetropis* + *Colocistis*)))))). A complete synonymic checklist of genera and species is also given, with **new synonymy** of the Cameron species ***Brachycistis tysias, Brachycistis dubitatus*** **and *Brachycistis sciron* under *Brachycistis alcanor* (Blake)**, and ***Brachycistis fulvilabris*** **and *Brachycistis arines* under *Brachycistis vigilax* Cameron**. In addition, ***Brachycistis ioachinensis*** **Bradley** is also **newly synonymized under *vigilax***.

Key words.—Tiphiidae, Brachycistidinae, *Acanthetropis, Brachymaya, Brachycistis, Brachycistellus, Colocistis, Dolichetropis, Hadrocistis, Paraquemaya, Sedomaya, Stilbopogon*

Nocturnal tiphiids in the Western Hemisphere all belong to the subfamily Brachycistidinae, which only occurs in the Americas. In the Palearctic and Afrotropical Regions nocturnal tiphiids are all members of the subfamily Myzininae. There has never been a monographic review of the Brachycistidinae, although a number of the genera have been at least partly revised (Kimsey and Wasbauer 1998a, 1998b, Wasbauer 1958, 1966, 1968a). Brothers (1975), Brothers and Carpenter (1993) and Kimsey (1991) gave Brachycistidinae status as the sister group of Tiphiinae. This monophyletic group is characterized by a number of distinctive modifications, including in the male the pronotum lacking a dorsal surface, edentate tarsal claws, ocelli generally enlarged, and forewing with abbreviated marginal and submedial cells, and in the female a single midtibial spur.

Brachycistidine wasps are thought to be difficult taxonomically because they lack distinctive coloration and the species appear structurally similar. However, the males have distinctive and informative modifications of the head, thorax, wing venation and genitalia. Most of the taxonomy of Brachycistidinae is based on males. Some aspects of the wing venation used to discriminate species and genera, such as the number of submarginal or discoidal cells, seem correlated with body size rather than higher taxon. The greatest taxonomic problem in this group is one shared by the Mutillidae: males and females are adapted for entirely different microhabitats and share few if any characteristics. Females are wingless and ant-like, lacking even ocelli. There are very few female brachycistidines in collections, as they are nocturnal and are not collected by common trapping methods. In Brachycistidinae this dichotomy has resulted in entirely different species and generic level nomenclature for males versus females. Mickel and Krombein (1942) described seven genera on the basis of females and there are currently 11 genera based on males. Wasbauer (1968b, 1971) associated some of the

Table 1. Character matrix for the brachycistidine genera based on male characteristics discussed in the text.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
Tiphia	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Stilbopogon	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0
Brachymaya	1	0	1	0	0	0	0	0	1	1	0	0	0	0	0	1	1	0	0	0	0	0	1	1
Hadrocistis	1	0	1	1	1	0	0	0	1	1	0	0	0	0	0	1	1	0	0	0	0	1	1	1
Brachycistina	1	0	1	1	1	0	0	0	1	1	0	0	0	0	0	1	1	0	0	0	0	0	1	0
Acanthetropis	1	1	2	0	0	1	1	1	1	1	1	1	1	1	1	2	0	0	0	1	1	0	1	0
Colocistis	1	1	2	0	0	1	1	1	1	1	1	0	1	1	1	2	0	1	0	1	0	0	0	0
Brachycistis	1	1	2	0	0	1	1	1	1	1	1	0	0	1	0	2	0	0	0	0	0	0	1	1
Brachycistellus	1	0	1	0	0	1	0	0	1	1	1	0	0	0	0	2	0	0	0	1	0	0	1	0
Dolichetropis	1	1	1	0	0	1	0	0	1	1	1	0	0	0	0	1	0	0	0	0	0	0	1	1
Paraquemaya	1	0	1	0	0	1	0	0	1	1	0	0	0	0	0	1	0	0	0	1	0	0	1	1
Sedomaya	1	1	1	0	0	1	0	1	1	1	1	0	0	0	0	1	0	0	0	1	0	0	1	1

type species of these female-based genera with males in the genus *Brachycistis*. Additional synonymies were made by Kimsey (2006). Clearly, more sex associations may be needed to eliminate extraneous generic and species names in this group, but this can probably only be accomplished by more intensive collecting efforts, DNA homologies, or by rearing once hosts are known. A complete synonymic checklist of the Brachycistidinae is given below.

MATERIALS AND METHODS

Specimens used in this study came from the Bohart Museum of Entomology, University of California, Davis (UCDC); Entomology Research Museum, University of California, Riverside (UCRC); the California Academy of Sciences, San Francisco (CAS), and the personal collection of M. S. Wasbauer. The species examined for this study are indicated in the checklist by an asterisk (*). Collection repositories cited in the checklist include: MCZ - Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts (S. Shaw); CU - Department of Entomology, Cornell University, Ithaca, New York (J. Liebherr); SMEK – Snow Entomological Museum, University of Kansas, Lawrence (R. Brooks); EMUS – Entomology Collection, Utah State University, Logan (T. Griswold); BMNH – The Natural History Museum, London, S. Lewis; LACM – Los Angeles County Museum of Natural History, Los Angeles, California (R. R. Snelling); AMNH – American Museum of Natural History, New York City, New York (J. M. Carpenter); ANSP - Philadelphia Academy of Sciences (D. Azuma); CAS - California Academy of Sciences, San Francisco (N. Penny); UMSP - University of Minnesota, St. Paul (J. C. Luhman); and NMNH – U. S. National Museum of Natural History, Smithsonian Institution, Washington, D. C. (A. S. Menke, K. V. Krombein). The Cameron *Brachycistis* types were borrowed from the Natural History Museum, London.

Male characters below were prepared using Winclada version 1.00.08 (Nixon 2002) and analyzed in Hennig86 (Farris 1988) and NONA version 2.0 (Goloboff 1999). The data matrix consisted of twenty-three male characters and 13 taxa (Table 1). The genus *Tiphia* was used to represent the sister group Tiphiinae as the outgroup. Species used in the analysis were selected to give the widest range of characteristics possible. However, once characters were coded it was found that multiple species from each genus were redundant and were therefore eliminated from the analysis as uninformative, resulting in a single exemplar species for each genus.

Characters.—

1. Antennal socket: rim simple (0), with ventral carinule or dilation (1). In the majority of tiphiids the antennal sockets are rimmed by a simple carina. This is also the case in *Stilbopogon* (Fig. 11). Therefore a simple antennal socket carina is considered primitive. In the other brachycistidine genera the socket carina has a ventrally pointing "tail", dilation or subsidiary carinule (Fig. 7).
2. Eye margin: flattened or evenly convex (0), emarginated (1). In *Tiphia* and the majority of brachycistidine genera the inner margin of male eye is flattened or convex. The remaining brachycistidine genera have the inner eye margin indented or emarginate (as in Fig. 7).
3. Clypeal shape: flat in profile (0), convex (1) or concave (2). In tiphiines the male clypeus is flat in profile. In the majority of brachycistidines the clypeus is convex and in *Acanthetropis*, *Brachycistis* and *Colocistis* the clypeus is concave in profile.
4. Maxillary palpal segments: normal (0), reduced (1). The normal number of maxillary palpal segments in tiphiids is six. In *Hadrocistis* the maxillary palp is polymorphic: 3 (*slanskyae*) or 5-segmented (*bicolor*). In *Brachycistina* the maxillary palp is 3-segmented.
5. Labial palpal segments normal (0), reduced (1). The normal number of labial palpal segments in tiphiids is four. In *Hadrocistis* the labial palp is polymorphic: 1-segmented in *slanskyae* and 2-segmented in *bicolor*. In *Brachycistina* the labial palp is 1-segmented.
6. Mandibular carina: absent (0), present (1). In the primitive form of the mandible, there are no external carinae, angles or projections (as in Fig. 11). In many brachycistidines the mandible has a longitudinal ridge on the outer surface extending from near the base to a subapical position (as in Fig. 2).
7. Frons: smooth above each antennal socket (0), with arcuate carina and apical warts (1). A peculiar modification of the frons can be seen in *Brachycistis*, *Acanthetropis* and *Colocistis* (Figs 2, 4, 7). In these genera there is a short crescentic carina above each antennal socket. In most the carina terminates on either end in a small wart or tubercle. This is a feature found only in this clade.
8. Hypostomal carina. Carina ending at or outside mandibular socket (0), ending inside mandibular socket (1). In the majority of brachycistines and in *Tiphia* the hypostomal carina terminates midway on or outside of the mandibular socket. The carina ends inside the mandibular socket in *Sedomaya*, *Brachycistis*, *Acanthetropis* and *Colocistis*.
9. Gular bridge: simple (0), with narrow expansion over base of tongue (1). Unlike the condition seen in tiphiines, in some brachycistidines the gula has a narrow expansion made up of a broadened hypostomal carina that overlaps the base of the tongue.
10. Pronotal dorsal surface: present (0), absent (1). In *Tiphia* and *Stilbopogon* the pronotum is dorsally expanded and the dorsal edge is planar with the scutum. In the rest of the Brachycistidinae, with the exception of two species of *Colocistis*, the pronotum lacks a dorsal surface and is substantially shorter than the strongly bulging scutum.
11. Stridulatory patch: absent (0), present (1). Most tiphiids lack any kind of stridulatory structure. However in the majority of brachycistidine genera males have a small stridulatory structure on the mesal surface of the forecoxa, consisting of a defined, slightly raised patch of dense fine ridges (Fig. 27). This feature occurs in

both major brachycistidine clades with a few notable, perhaps secondary, absences in *Brachycistina* and *Paraquemaya*.

12. Scrobal sulcus: absent (0), present (1). In brachycistidines a scrobal sulcus is only present in *Acanthetropis*.
13. Hindwing discoidal veinlet: present (0), absent (1). All of the brachycistidine genera, except *Acanthetropis* and *Colocistis*, have a short discoidal veinlet present on the hindwing.
14. Propodeal transverse carina: absent (0), present (1). A transverse carina dividing the dorsal from the posterior surfaces of the propodeum is seen only in *Acanthetropis*, *Colocistis* and *Brachycistis*.
15. Propodeum dorsomedially: convex (0), longitudinally grooved (1). Another modification of the propodeum is the presence of a broad longitudinal groove extending posteriorly from the scutellar margin along the dorsal surface of the propodeum. This feature occurs in *Colocistis* and *Acanthetropis*.
16. Metapleural lobes: fused (0), digitate (1) or broadly rounded (2). Tiphiines have the metapleural lobes fused into a platform between the midcoxae. In the Brachycistidinae the metapleural lobes are either small and slender or flattened and apically rounded.
17. Hindcoxal dorsal carina: present (0), absent (1). Throughout the Tiphiidae the hindcoxa normally has a dorsal carina that extends from the coxal base towards the apex. This carina is absent in *Brachymaya*, *Hadrocistis* and *Brachycistina*.
18. Hindcoxal ventromedial carina: absent (0), present (1). This is a unique feature in *Colocistis*.
19. Basal petiolar carina: present (0), absent (1). In the Tiphiinae, and most genera of Brachycistidinae the basal metasomal tergum has a strongly expanded lateral carina often completely ringing the tergum, which may serve to protect the petiolar socket. In *Stilbopogon* this carina is absent and the tergal base is simple where it inserts into the petiolar socket.
20. Sternum I basal longitudinal carina present (0), absent (1). Tiphiines have a short longitudinal carina extending down the middle of the basal gastral sternum from the base of the plate. This condition is also seen in *Acanthetropis*, *Brachycistellus* and *Colocistis* (Figs 28, 30). In the derived condition the first gastral sternum is smooth basally with no trace of a carina (Fig. 29).
21. Sternum II: simple (0), with medial keel (1). The second gastral sternum is generally unmodified, although *Dolichetropis* have a transverse submedial carina. All species of *Acanthetropis* have a longitudinal keel or fold extending longitudinally from the base. In most *Acanthetropis* species this structure consists of a sharp posteriorly hooked, keel-like carina in the middle of this sternum. However, in *A. lamellatus* this structure consists of a longitudinal fold ending in a transverse lamella.
22. Epipygium shape: rounded laterally (0), laterally carinate or folded (1). The epipygium, or apical metasomal tergum, is generally narrowed and evenly rounded apically in the Tiphiidae. In brachycistidines the epipygium can be sharply folded or carinate laterally.
23. Digitus apex: broadly rounded (0), apically elongate and acute (1). In tiphiines the volsella is typically fist-shaped, with the digitus and cuspis forming short rounded apical lobes (Figs 32, 35, 41, 46). However, in the majority of brachycistidine genera the digitus is greatly elongate and digitate, or awl-shaped, extending apically (as in Figs 36, 37).
24. Volsellar inner margin: smooth (0), denticulate (1). *Brachymaya*, *Hadrocistis*, *Brachycistis*, *Dolichetropis*, *Paraquemaya* and *Sedomaya* the inner margin of

the volsella is denticulate (as in Figs 36, 38). This surface is smooth in the remaining genera and in *Tiphia*.

RESULTS

Phylogenetic analyses.—Phylogenetic analysis of the matrix yielded a single optimal tree (Fig. 1A), with a tree length of 32, CI of 78 and RI of 83. Multistate characters were treated as non-additive and were equally weighted. Of these six proved uninformative as they coded for a single genus. Other characters used in the key, such as the orientation of the hindwing tCu vein and length of the forewing R vein, were eliminated from consideration early on because they only coded for a single genus. Bootstrap values were calculated after eliminating suboptimal trees, resulting in the single tree in Fig. 1B. The values show strong to moderate support for most of the branches. *Stilbopogon* was found to be the basal taxon in the subfamily in all analyses. The rest of the genera fell into two well supported clades. One clade consisting of *Brachymaya*, *Hadrocistis* and *Brachycistina*, based on the lack of a dorsal coxal carina. The second clade contains the remaining genera, based on the presence of a mandibular carina and a T-shaped carina at the base of metasomal sternum I. The resulting generic relationships are *Stilbopogon* + (*Brachymaya* + (*Hadrocistis* + *Brachycistina*)) + (*Paraquemaya* + (*Brachycistellus* + (*Dolichetropis* + (*Sedomaya* + (*Brachycistis* + (*Acanthetropis* + *Colocistis*)))))).

KEY TO MALES OF THE GENERA OF BRACHYCISTIDINAE

1	Forewing with two discoidal cells (as in Fig. 14)	2
-	Forewing with one discoidal cell (as in Fig. 15)	6
2	Sternum II with medial longitudinal ridge or keel extending posteriorly from base; forewing R vein extending along costal margin more than two-thirds length of stigma (Fig. 14)	*Acanthetropis* Wasbauer
-	Sternum II without medial ridge; forewing R vein extending along costal margin for less than two-thirds the length of stigma or not reaching costal margin at all (as in Figs 15, 17)	3
3	Mandible without longitudinal carina on external surface and with two apical teeth (Fig. 5); maxillary and labial palpi highly reduced barely visible between mandibles, with three and two or fewer palpomeres respectively	*Brachycistina* Malloch
-	Mandible with longitudinal carina on external surface and with three apical teeth (as in Fig. 4); maxillary and labial palpi clearly visible beneath head, extending as far as occipital carina or further, with six and four palpomeres respectively	4
4	Maxillary palpi slender and short, barely reaching occipital carina; forewing R vein extending along costal margin between one half and two-thirds stigmal length (Fig. 20)	*Dolichetropis* Wasbauer
-	Maxillary palpi robust and long, extending well beyond underside of head; forewing R vein extending along costal margin less than one-third stigmal length or not even reaching costal margin	5
5	Sternum I with short medial longitudinal carina extending posteriorly from base; forewing tCu-1 arising at or before basal third of first submarginal cell (Fig. 19); digitus with short, broadly rounded apex (Figs 39, 40)	*Colocistis* Krombein
-	Sternum I smooth subbasally without medial carina; forewing tCu-I arising beyond basal third of first submarginal cell (Fig. 17); digitus with elongate, acute apex (Figs 36, 37)	*Brachycistis* Fox

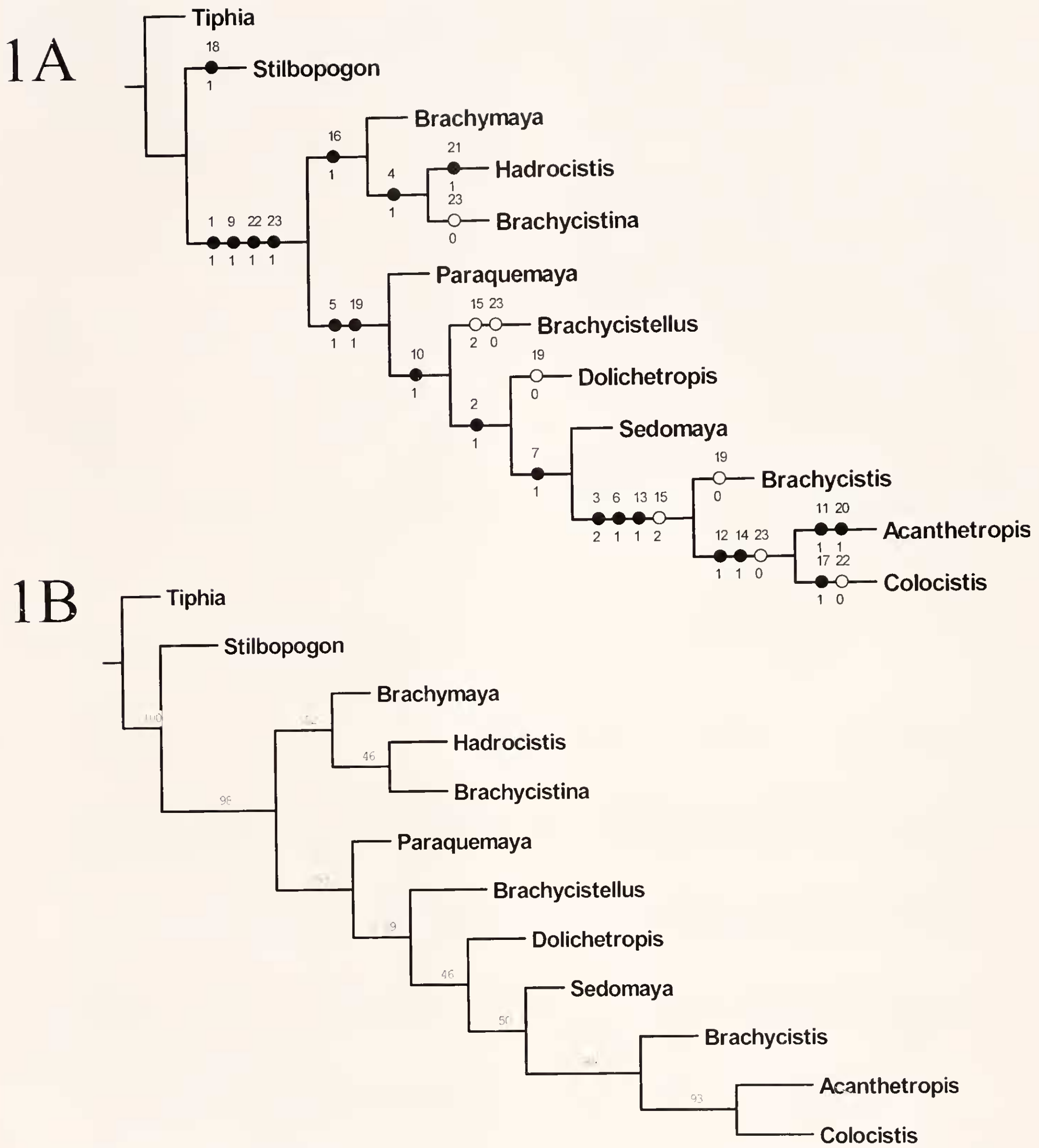
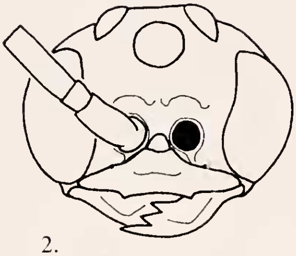


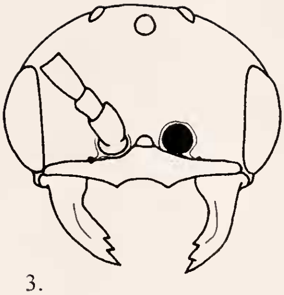
Fig. 1. Cladograms of relationships among the ten genera of Brachycistidinae based on male characteristics. Fig. 1A. Tree showing relationships among the genera. Numbers refer to characteristics discussed in the text. Fig. 1B. Tree showing Bootstrap values.

6 Hindwing cubitus forming a nearly straight line with transverse cubitus, meeting it at more 130° angle or greater (Fig. 23); digitus short, blunt, without elongate apex (Figs 45, 46) . . . . *Stilbopogon* Mickel and Krombein

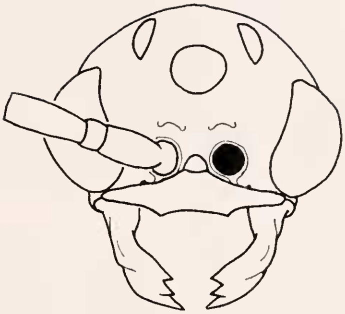
- Hindwing cubitus arcuately curved, meeting transverse cubitus at less than 130° angle; digitus usually with elongate, acute apex 7



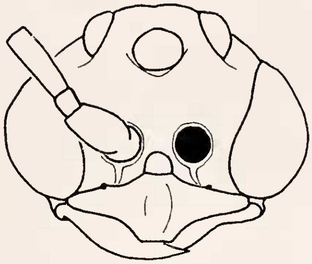
2.
Acanthetropis aequalis



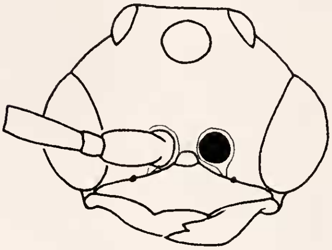
3.
Brachycistellus figitiformis



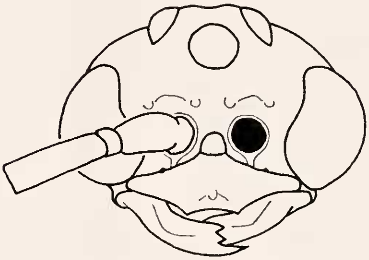
4. *Brachycistis alcanor*



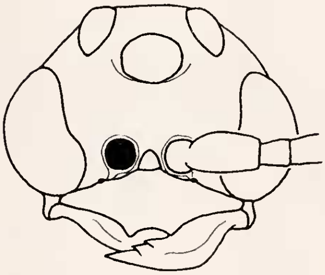
5. *Brachycistina acuta*



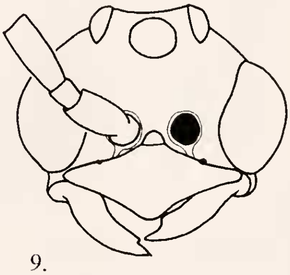
6. *Brachymaya mexicana*



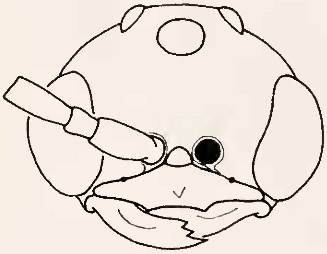
7. *Colocistis crassa*



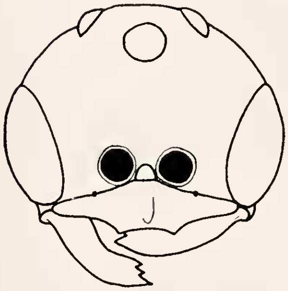
8.
Dolichetropis flavida



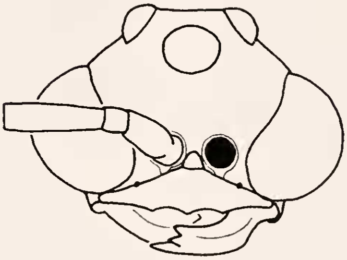
9.
Hadrocistis slanskyae



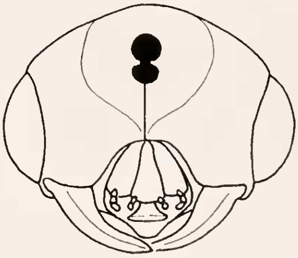
10. *Paraquemaya pallida*



11. *Quemaya marcida*

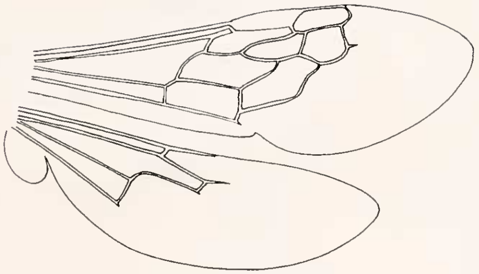


12. *Sedomaya glamisensis*

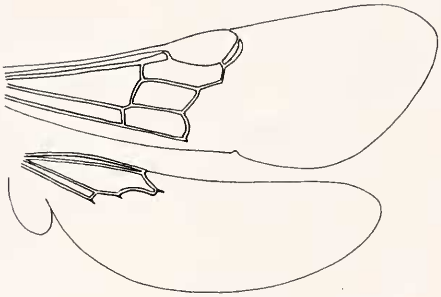


13. *Hadrocistis slanskyae*

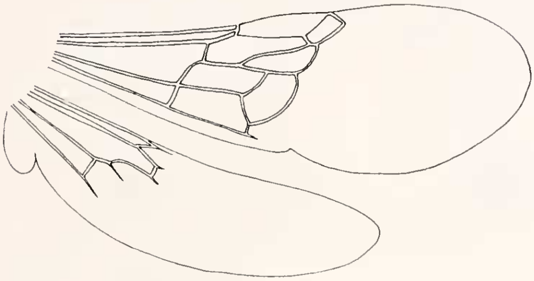
Figs 2–13. Male head, with one or both antennae removed. Figs 2–12. Front view. Fig. 13. Ventral view.



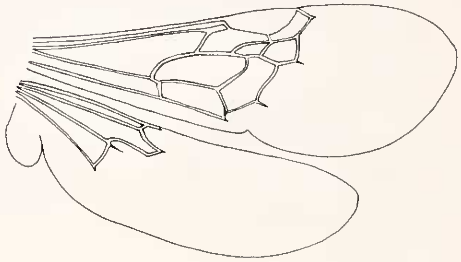
14. *Acanthetropis aequalis*



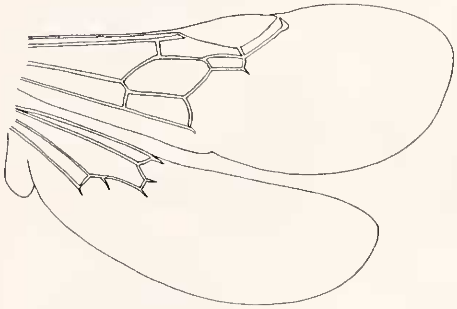
15. *Brachycistellus figitiformis*



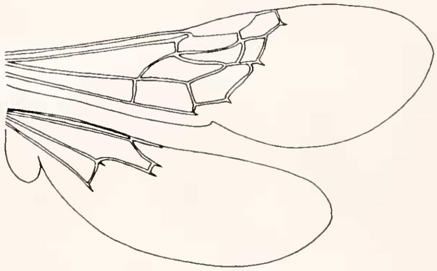
16. *Brachycistina acuta*



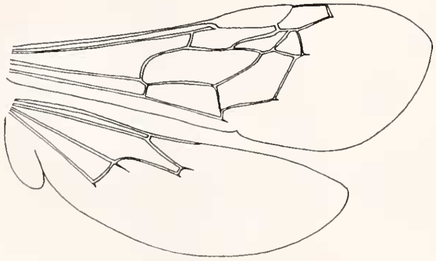
17. *Brachycistis alcanor*



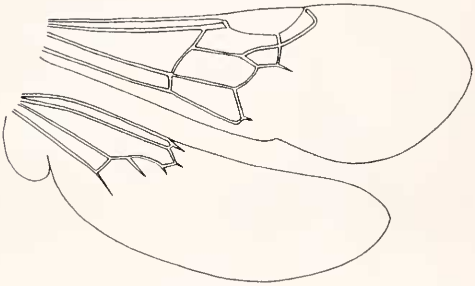
18. *Brachymaya mexicana*



19. *Colocistis stygia*

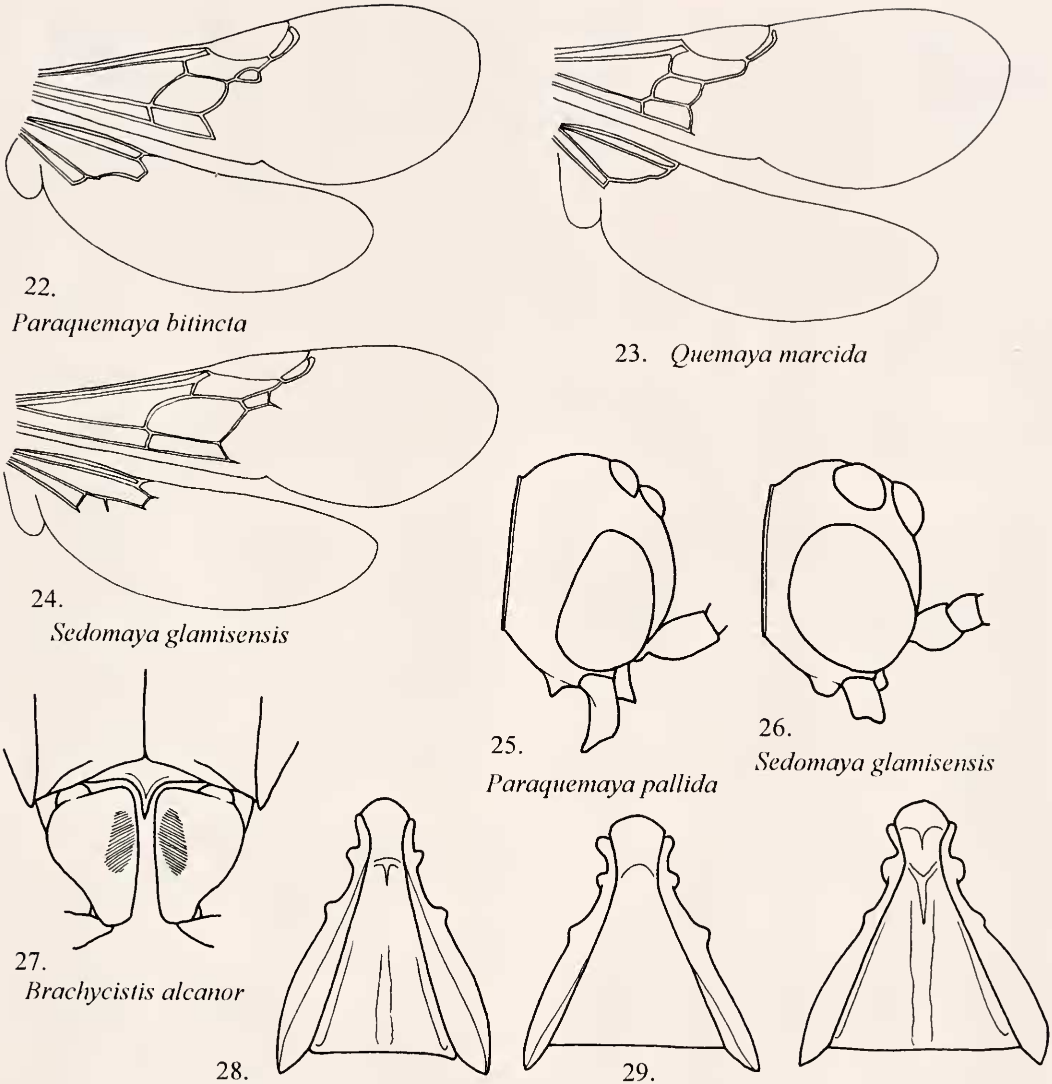


20. *Dolichetropis flavida*



21. *Hadrocistis slanskyae*

Figs 14–21. Male fore and hindwings.



22.
Paraquemaya bitincta

23. *Quemaya marcida*

24.
Sedomaya glamisensis

25.
Paraquemaya pallida

26.
Sedomaya glamisensis

27.
Brachycistis alcanor

28.
Acanthetropis lamellatus

29.
Dolichetropis flavida

30. *Colocistis stygia*

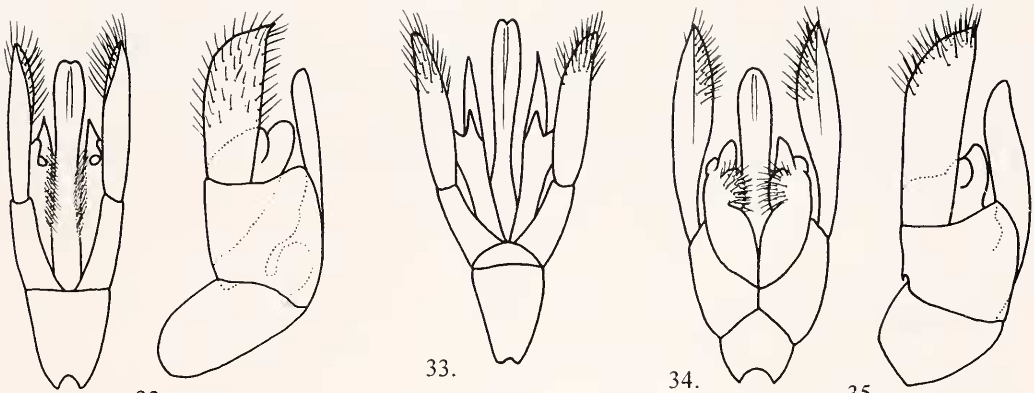
Figs 22–24. Male fore and hindwings. Figs 25, 26. Lateral view of male head. Fig. 27. Ventral view of prothorax and forecoxae. Figs 28–30. Ventral view of basal gastral sternum.

7 Palpi highly reduced, shorter than oral fossa, with fewer than five maxillary and three labial palpomeres (Fig. 13) . . . . *Hadrocistis* Wasbauer

- Palpi large, much longer than oral cavity; with six maxillary and four labial palpomeres 8

8 Propodeum heavily sculptured with transverse carina separating dorsal and posterior surfaces; compound eyes and ocelli not enlarged, distance between midocellus and nearest eye margin 4–5 MOD (Fig. 3) . . . . *Brachycistellus* Baker

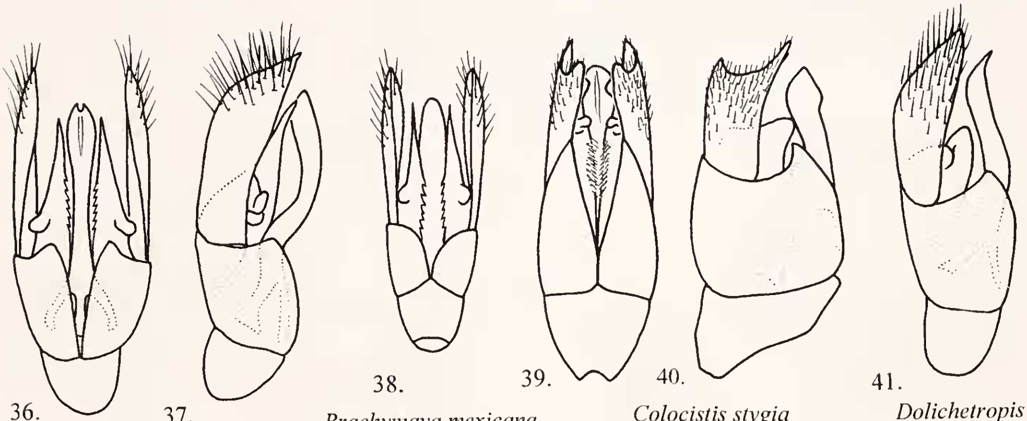
- Propodeum nearly smooth, without transverse carina; compound eyes and ocelli enlarged, distance between midocellus and nearest eye margin not more than 3 MOD 9



31. 32.
Acanthetropis lamellatus

33.
Brachycistellus figitiformis

34. 35.
Brachycistina acuta

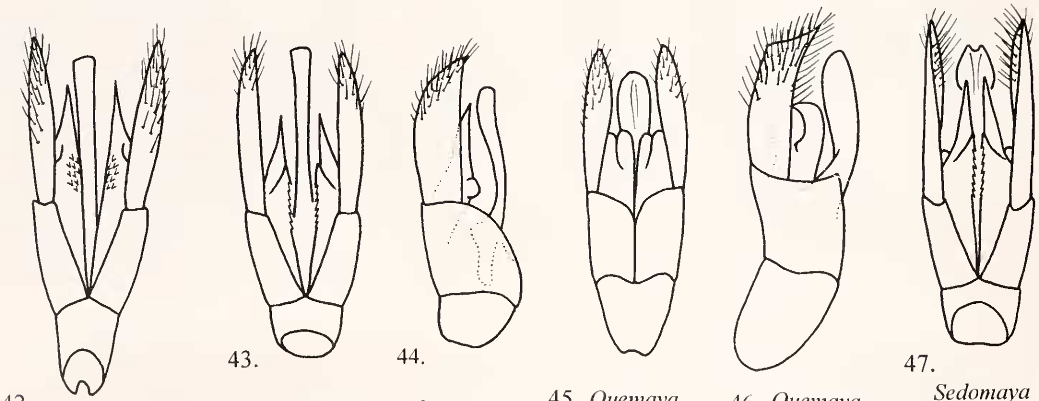


36. 37.
Brachycistis alcanor

38.
Brachymaya mexicana

39. 40.
Colocistis stygia

41.
Dolichetropis flavidus



42.
Hadrocistis bicolor

43. 44.
Paraquemaya bitincta

45. *Quemaya paupercula*

46. *Quemaya megalops*

47.
Sedomaya glamisensis

Figs 31–47. Male genital capsule. Figs 31, 33, 34, 36, 38, 39, 42, 43, 45, 47. Ventral view. Figs 32, 35, 37, 40, 44, 46. Lateral view.

9 Mandible bidentate, without longitudinal carina on external surface (Fig. 6); oral carina simple and gular area at base of mandible (traversed by oral carina) not dilated or bulging . . . . *Brachymaya* Kimsey and Wasbauer

- Mandible tridentate, with longitudinal carina on external surface; oral carina expanded into tooth or lamella (Fig. 25) or gular area (traversed by oral carina) bulging near base of mandible (Fig. 26) 10

10 Oral carina expanded into lamellate projection or tooth near mandibular base, gular area not bulging near base of mandible (Fig. 25); forecoxa without stridulatory patch on mesal surface . . . . *Paraquemaya* Kimsey and Wasbauer

- Oral carina unmodified, gular area strongly bulging near base of mandible (Fig. 26); forecoxa with stridulatory patch on mesal surface . . . . *Sedomaya* Kimsey and Wasbauer

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CHECKLIST OF THE BRACHYCISTIDINAE

Genus *Acanthetropis* Wasbauer

Figs 2, 14, 28, 31, 32

Acanthetropis Wasbauer 1958:139. Type species: *Acanthetropis lamellatus* Wasbauer 1958:140. Original designation. Distribution: USA: South Dakota, south to Baja California Sur, west to California.

Species List

aequalis (Fox) 1899:284. (*Brachycistis*). Holotype male; Nevada (ANSP).*

lamellatus Wasbauer 1958:140. (*Acanthetropis*). Holotype male; Mexico: Baja California, La Paz (CAS).*

noctivaga (Bradley) 1917:272. (*Brachycistis*). Holotype male; USA: Nevada, Las Vegas (CU).*

normalis (Malloch) 1917:8. (*Brachycistis*). Holotype male; USA: South Dakota, Cedar Pass (NMNH).*

Genus *Brachycistellus* Baker

Figs 3, 15, 33

Brachycistellus Baker 1909:177. Type species: *Brachycistellus figitiformis* Baker 1909:177. Original designation. Distribution: USA: southern California.

Species List

figitiformis (Baker) 1909:178. (*Brachycistis*). Holotype male; USA: California, Claremont (NMNH).*

Genus *Brachycistina* Malloch

Figs 5, 16, 34, 35

Brachycistina Malloch 1926:25. Type species *Brachycistis acuta* Malloch 1926:25. Described as a subgenus of *Brachycistis* Fox. Elevated by Wasbauer (1966). Distribution: USA: Arizona.

Species List

acuta Malloch 1926:25. (*Brachycistina*). Holotype male; USA: Arizona, Arlington (NMNH).*

Genus *Brachycistis* Fox

Figs 4, 17, 27, 36, 37

Brachycistis Fox 1893:7. Type species: *Brachycistis petiolatus* Fox 1893:8. Original designation. Distribution: southwestern North America (USA, northwestern Mexico).

Brachycistus (!) Cockerell and Casad. 1894:295.

Glyptomeopa Ashmead 1898:251. Type species: *Glyptometopa americana* Ashmead 1898:251. Monobasic. Synonymized by Wasbauer 1968.

Glytometopa (!) Fox 1899:289.

Brachycystis (!) Viereck 1906:289.

Bruesiella Mann 1914:182. Type species: *Bruesiella formicaria* Mann 1914:182. Original designation. Synonymized by Kimsey 2006.

Eurycros Mickel & Krombein 1942:666. Type species: *Eurycros furtivus* Mickel & Krombein 1942:667. Orig. designation. Synonymized by Krombein 1967.

Aulacros Mickel & Krombein 1942:664. Type species: *Aulacros latior* Mickel & Krombein 1942:665. Original designation. Synonymized by Kimsey 2006.

Species List

- *agama* (Dalla Torre) 1897:7. (*Mutilla*). Replacement name for *atrata* (Blake) 1879. Nec *Mutilla atratus* Linnaeus 1767:966.
  - *atrata* (Blake) 1879:253. (*Agama*). Holotype male; USA: Nevada (ANSP). Synonymized by Wasbauer 1966.
  - *contiguus* Fox 1899:282. (*Brachycistis*). Syntype males; USA: Nevada (ANSP). Synonymized by Wasbauer 1966.
  - *nigritus* Fox 1899:282. (*Brachycistis*). Syntype males; USA: Nevada, Washington (ANSP). Synonymized by Wasbauer 1966.
  - *nudus* Fox 1899:281. (*Brachycistis*). Holotype male; USA: California (ANSP). Synonymized by Wasbauer 1966.
  - *francisca* (Mickel & Krombein) 1942:656. (*Glyptometopa*). Holotype female; USA: California, San Francisco (CAS). Synonymized by Wasbauer 1968.
- *alcanor* (Blake) 1879:264. (*Agama*). Holotype male; USA: Arizona (ANSP).*
  - *tysias* Cameron 1900:396. Holotype male; Mexico: northern Sonora (BMNH).* **New synonymy.**
  - *dubitatus* Cameron 1900:397. (*Brachycistis*). Holotype male; Mexico: northern Sonora (BMNH).* **New synonymy.**
  - *sciron* Cameron 1900:400. (*Brachycistis*). Holotype male; Mexico: northern Sonora (BMNH).* **New synonymy.**
  - *cremastogaster* Melander 1903:329. (*Brachycistis*). Holotype male; Texas (Repository unknown). Synonymized by Wasbauer 1966.
- *ampla* (Blake) 1879:252. (*Agama*). Holotype male; USA: Colorado (ANSP).
- *americana* (Ashmead) 1898:251. (*Glyptometopa*). Holotype female; USA: California, Alameda Co. (NMNH).
- *arenivaga* Bradley 1917:269. (*Brachycistis*). Holotype male; USA: California, Imperial Co. (CU).*
  - *eriopis* Bradley 1917:266. (*Brachycistis*). Holotype male: USA: California, Imperial Co., Calexico (CU). Synonymized by Wasbauer 1966.*
- *carinata* Fox 1899:283. (*Brachycistis*). Holotype male; USA: California (ANSP).
- *convergens* (Mickel & Krombein) 1942:657. (*Glyptometopa*). Holotype female; USA: California, Santa Monica (NMNH).
- *convexa* Wasbauer 1966:51. (*Brachycistis*). Holotype male; USA: California, Imperial Co. (MCZ).
- *cruenta* Wasbauer 1966:53. (*Brachycistis*). Holotype male; USA: Texas, Nueces Co., Corpus Christi (CAS).*
- *curvata* Malloch 1926:16. (*Brachycistis*). Holotype male; USA: Arizona (NMNH).*
- *davidi* Wasbauer 1966:56. (*Brachycistis*). Holotype male; USA: Texas, Jeff Davis Co. (CAS).
- *elegantula* Cockerell & Casad 1894:295. (*Brachycistis*). Holotype male; USA: New Mexico, Dona Ana Co., Las Cruces (NMNH).*
- *exornatus* Cameron 1900:402. (*Brachycistis*). Holotype male; Mexico: northern Sonora (BMNH, type lost?).
- *formicaria* (Mann) 1914:182. (*Bruesiella*). Holotype female; Mexico: Hidalgo (MCZ).
- *furtivus* (Mickel & Krombein) 1942:667. (*Eurycros*). Holotype female; USA: Arizona, Tucson (UMSP).
- *glabrella* Cresson 1865b:441. (*Brachycistis*). Holotype male; USA: New Mexico, Sandoval Co. (ANSP).*
  - *dentata* Bradley 1917:263. (*Brachycistis*). Holotype male; USA: New Mexico, Jemez Spr. (CU). Synonymized by Wasbauer 1966.
  - *micrommata* Bradley 1917:265. (*Brachycistis*). Holotype male; USA: California, Alameda Co. (CU). Synonymized by Wasbauer 1966.
  - *utahensis* Malloch 1926:17. (*Brachycistis*). Holotype male; USA: Utah (NMNH). Synonymized by Wasbauer 1966.
  - *dakotensis* Malloch 1926:20. (*Brachycistis*). Holotype male; USA: North Dakota, Edgemont (NMNH). Synonymized by Wasbauer 1966.
  - *melanocephala* Malloch 1926:19. (*Brachycistis*). Holotype male; USA: Utah, Uinta National. Forest (NMNH). Synonymized by Wasbauer 1966.
- *idiotes* Cockerell 1895a:63. (*Brachycistis*). Holotype male; USA: New Mexico (Repository unknown).
- *imitans* Malloch 1926:23. (*Brachycistis*). Holotype male; USA: California, Los Angeles Co. (NMNH).*
- *inaequalis* Fox 1899:282. (*Brachycistis*). Lectotype male (design by Krombein 1954); USA: California, Los Angeles Co. (NMNH).*
  - *nevadensis* Fox 1899:283. (*Brachycistis*). Holotype male; USA: Nevada (ANSP). Synonymized by Wasbauer 1966.*
  - *nocticola* Bradley 1917:289. (*Brachycistis*). Lap sus calumni: name used in error in Explanation of Figures, no holotype indicated or

description given, as discussed by Krombein 1954. Synonymized by Wasbauer 1966.

indiscreta Fox 1899:284. (*Brachycistis*). Holotype male; USA: Arizona, Cochise Co., Wilcox (NMNH).*

stictinota Viereck 1906:190. (*Brachycistis*). Holotype male; USA: Kansas: Clark Co. (SMEK). Synonymized by Wasbauer 1966.*

juncea Wasbauer 1966:35. (*Brachycistis*). Holotype male; USA: California, San Bernardino (CAS).

lacustris Malloch 1926:24. (*Brachycistis*). Holotype male; USA: Nevada, Pyramid Lk. (NMNH).*

hurdi Wasbauer 1966:39. (*Brachycistis*). Holotype male; USA: California, Riverside Co. (CAS). Described as a subspecies of *lacustris* Malloch. **New synonymy.**

latior (Mickel & Krombein) 1942:665. (*Aulacros*). Holotype female; USA: California, Palm Springs (CAS).

linsleyi Wasbauer 1966:21. (*Brachycistis*). Holotype male; Arizona: Globe (CAS).*

longula Wasbauer 1966:39. (*Brachycistis*). Holotype male; USA: California, Riverside Co. (CAS).

nitida (Cresson) 1875:710. (*Agama*). Holotype male; Colorado (ANSP).

lepidus (Blake) 1886:269. (*Photopsis*). Holotype male; Colorado (ANSP). Synonymized by Wasbauer 1966.*

nitida (Blake) 1886:267. (*Photopsis*). Holotype male; Colorado (ANSP). Synonymized by Wasbauer 1966.*

sobrina (Blake) 1886:268. (*Photopsis*). Holotype male; Colorado (ANSP). Synonymized by Wasbauer 1966.

petiolata Fox 1893:8. (*Brachycistis*). Holotype male; Mexico: Baja California, Calmalli Mines (CAS).*

gaudii Cockerell 1901:340. (*Brachycistis*). Lectotype male (designated herein); USA: California, San Diego Co., La Jolla (NMNH). Synonymized by Wasbauer 1966.

parva Malloch 1926:14. (*Brachycistis*). Holotype male; USA: California (NMNH). Synonymized by Wasbauer 1966.

protracta Bradley 1917:270. (*Brachycistis*). Holotype male; USA: Arizona, Phoenix (ANSP).

semiatra Malloch 1926:24. (*Brachycistis*). Holotype male; USA: Washington, Adams Co., (NMNH)

subquadrata Fox 1899:282. (*Brachycistis*). Holotype male; USA: California, San Diego Co., San Diego (ANSP).

intermedia Malloch 1926:18. (*Brachycistis*). Holotype male; USA: California, San Diego Co., San Diego (NMNH). Synonymized by Wasbauer 1966.

texana Malloch 1926:12. (*Brachycistis*). Holotype male; USA: Texas, Cotulla (NMNH).*

timberlakei Wasbauer 1966:70. (*Brachycistis*). Holotype male; USA: California, San Diego Co. (CAS).

triangularis Fox 1899:284. (*Brachycistis*). Holotype male; USA: Arizona (ANSP).*

verticalis Malloch 1926:19. (*Brachycistis*). Holotype male; USA: Arizona, Fort Grant (NMNH).*

vigilax Cameron 1900:397. (*Brachycistis*). Holotype male; Mexico: northern Sonora (BMNH).

fulvilabris Cameron 1900:399. (*Brachycistis*). Holotype male; Mexico: northern Sonora (BMNH).* **New synonymy.**

arines Cameron 1900:401. (*Brachycistis*). Holotype male; Mexico: northern Sonora (BMNH).* **New synonymy.**

ioachinensis Bradley 1917:267. (*Brachycistis*). Holotype male; USA: California, Fresno Co., Coalinga (CU).* **New synonymy.**

washingtona Malloch 1926:21. (*Brachycistis*). Holotype male; USA: Washington, Ritzville (NMNH). Synonymized by Wasbauer 1966.*

subcarinata Malloch 1926:11. (*Brachycistis*). Holotype male; USA: Arizona, Higley (NMNH). Synonymized by Wasbauer 1966.*

rugosa Malloch 1926:11. (*Brachycistis*). Holotype male; USA: Nevada, Golconda (NMNH). Synonymized by Wasbauer 1966.*

nigrifrons Malloch 1926:16. (*Brachycistis*). Holotype male; USA: Arizona: Graham Mount., Ash Crk. (NMNH). Synonymized by Wasbauer 1966.*

Genus *Brachymaya* Kimsey & Wasbauer

Figs 6, 18, 38

Brachymaya Kimsey & Wasbauer 1998b:66. Type species: *Brachymaya mexicana* Kimsey & Wasbauer 1998:67. Original designation. Distribution. USA: Baja California.

Species List

mexicana Kimsey & Wasbauer 1998b:67. (*Brachymaya*). Holotype male; Mexico: Baja California, San Augustine (LACM).

Genus *Colocistis* Krombein

Figs 7, 19, 30, 39, 40

Colocistis Krombein 1942:65. Type species: *Colocistis pilosa* Krombein 1942:66. Original designation. Distribution: USA: California, Arizona.

Aglyptacros Mickel & Krombein 1942:669. Type species: *Aglyptacros paxillatus* (Mickel & Krombein) 1942:673. Original designation. Synonymized by Kimsey 2006

Species List

brevis (Fox) 1899:285. (*Brachycistis*). Holotype male; USA: California (NMNH, lost?),*

castanea (Cresson) 1865a:388. (*Brachycistis*). Holotype male; USA: California (ANSP).*

crassa (Bradley) 1917:277. (*Brachycistis*). Holotype male; USA: California, Fresno Co., Coalinga (CU).*

eremi (Bradley) 1917:279. (*Brachycistis*). Holotype male; USA: California, Imperial Co., Calexico (CU).

paxillatus (Mickel & Krombein) 1942:673. (*Aglyptacros*). Holotype female; USA: Colorado, La Junta (NMNH).

pilosa Krombein 1942:66. (*Colocistis*). Holotype male; USA: California, San Diego Co., San Diego (NMNH).*

segredentatus (Mickel & Krombein) 1942:671. (*Aglyptacros*). Holotype female; USA: Arizona, Benson (MCZ).

sulcatus (Mickel & Krombein) 1942:674. (*Aglyptacros*). Holotype female; USA: Texas, Valentine (SMEK).

stygia (Bradley) 1917:276. (*Brachycistis*). Holotype male; USA: Arizona, Nogales (CU).*

thermarum (Bradley) 1917:274. (*Brachycistis*). Holotype male; USA: Arizona, Hot Springs (CU).

Genus *Dolichetropis* Wasbaue

Figs 8, 20, 29, 41

Dolichetropis Wasbauer 1968a:191. Type species: *Dolichetropis flavida* Wasbauer 1968a:192. Original designation. Distribution: Mexico: Baja California Sur.

Species List

flavida Wasbauer 1968a:192. (*Dolichetropis*). Holotype male; Mexico: Baja California Sur, San Ignacio (CAS).*

Genus *Glyptacros* Mickel & Krombein

Glyptacros Mickel & Krombein 1942:660. Type species: *Glyptacros angustior* Mickel & Krombein 1942:660. Original designation. Distribution. Southwestern USA: California, Arizona, Utah, Wyoming, New Mexico, Texas; Mexico: Baja California Sur, Chihuahua, Hidalgo, Sonora.

Xeroglypta Mickel & Krombein 1942:663. Type species: *Xeroglypta egregia* Mickel & Krombein 1942:663. Original designation. Synonymized by Kimsey 2006.

Astigmometopa Mickel & Krombein 1942:668. Type species: *Astigmometopa emarginata* Mickel & Krombein 1942:668. Original designation. Synonymized under *Brachycistis* by Wasbauer 1971. Removed from synonymy under *Brachycistis* and synonymized under *Glyptacros* by Kimsey 2006.

Species List

angustior Mickel & Krombein 1942:660. (*Glyptacros*). Holotype female; USA: Arizona (ANSP).

ashmeadi Mickel & Krombein 1942:661. (*Glyptacros*). Holotype female; no locality given (NMNH).

egregia (Mickel & Krombein) 1942:663. (*Xeroglypta*). Holotype female; USA: California, Palm Springs (UMSP).

emarginata (Mickel & Krombein) 1942:668. (*Astigmometopa*). Holotype female; USA: Texas, Valentine (SMEK).

eureka (Banks) 1912:202. (*Glyptometopa*). Holotype female; USA: Arizona, Palmerlee (MCZ).

Genus *Hadrocistis* Wasbauer

Figs 9, 13, 21, 42

Hadrocistis Wasbauer 1968a:185. Type species: *Hadrocistis bicolor* Wasbauer 1968a:187. Original designation. Distribution: USA: California, Imperial Co.; Mexico: Baja California, Sinaloa.

Species List

bicolor Wasbauer 1968a:187. (*Hadrocistis*). Holotype male; USA: California, Imperial Co., 6 mi w Glamis (CAS).*

slanskyae Wasbauer 1968a:188. (*Hadrocistis*). Holotype male; USA: California, Imperial Co., 6 mi w Glamis (CAS).*

Genus *Paraquemaya* Kimsey & Wasbauer

Figs 10, 22, 25, 43, 44

Paraquemaya Kimsey and Wasbauer 1998b:67. Type species: *Paraquemaya pallida* Kimsey & Wasbauer 1998:71. Distribution. USA: Arizona; Mexico: Baja California Sur, Sonora.

Species List

bajaensis Kimsey and Wasbauer 1998b:69. (*Paraquemaya*). Holotype male; Mexico: Baja California Sur, 14 mi s El Arco (UCRC).*

bitincta Kimsey and Wasbauer 1998b:70. (*Paraquemaya*). Holotype male; USA: Arizona, Pima Co., Organ Pipe (UCRC).*

maxima Kimsey and Wasbauer 1998b:71. (*Paraquemaya*). Holotype male; Mexico: Sonora, 22 km se Quitovac (UCRC).*

pallida Kimsey and Wasbauer 1998b:71. (*Paraquemaya*). Holotype male; Mexico: Baja California Sur, 4 mi wsw Miraflores (UCDC).*

Genus *Sedomaya* Kimsey & Wasbauer

Figs 12, 24, 26, 47

Sedomaya Kimsey & Wasbauer 1998b:72. Type species: *Sedomaya glamisensis* Kimsey & Wasbauer. Original designation. Distribution. USA: California, Imperial Co.

Species List

glamisensis Kimsey & Wasbauer 1998b:72. (*Sedomaya*). Holotype male; USA: California, Imperial Co., Glamis (UCDC).

Genus *Stilbopogon* Mickel & Krombein

Figs 11, 23, 45, 46

Stilbopogon Mickel & Krombein 1942:658. Type species: *Stilbopogon alutacea* Mickel & Krombein 1942:659. Original designation. Synonymized by Wasbauer 1971 under *Brachycistis* Fox. Distribution. USA: California, Nevada, Arizona, New Mexico, Texas; Mexico: Baja California, Sonora; Costa Rica: Guanacaste; Colombia: Magdalena.

Quemaya Pate 1947:139. Type species: *Brachycistis paupercula* Bradley 1917:282. Original designation. Synonymized by Kimsey 2006.

Species List

alutacea Mickel & Krombein 1942:659. (*Stilbopogon*). Holotype female; USA: New Mexico, Deming (NEW YORK).

arenicola (Wasbauer) 1967:169. (*Quemaya*). Holotype male; USA: California, Imperial Co., 6 mi nw Glamis (CAS).*

confusa (Kimsey & Wasbauer) 1998b:42. (*Quemaya*). Holotype male; Mexico: Sonora, 6 km nnw San Carlos (UCDC).*

costaricana (Kimsey & Wasbauer) 1998b:43. (*Quemaya*). Holotype male; Costa Rica: Guanacaste Prov., 14 km s Cañas (EMUS).*

eurekensis (Kimsey & Wasbauer) 1998b:43. (*Quemaya*). Holotype male; USA: California, Inyo Co., Eureka Valley, dunes (UCDC).*

inermis (Malloch) 1924:23. (*Brachycistis*). Holotype male; USA: Arizona: Higley (NMNH).*

marcida (Bradley) 1917:283 (*Brachycistis*). Holotype male; USA: California, Imperial Co. (CU).*

megalops (Kimsey & Wasbauer) 1998b:44. (*Quemaya*). Holotype male; USA: California, Riverside Co., 5 mi nw Desert Center (UCDC).*

mexicana (Kimsey & Wasbauer) 1998b:43. (*Quemaya*). Holotype male; Mexico: Baja California, 1 km s El Rosario (UCDC).*

paupercula (Bradley) 1917:282. (*Brachycistis*). Holotype male; USA: California, Imperial Co. (CU).*

perpunctata (Cockerell) 1895b:291. (*Brachycistis*). Holotype male; USA: New Mexico, Dona Ana Co., Las Cruces (Repository unknown).

sonorensis (Kimsey & Wasbauer) 1998b:46. (*Quemaya*). Holotype male; Mexico: Sonora, 6 km nnw San Carlos (UCDC).*

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